

EFFECTS OF CROWDING ON WING MORPHOGENESIS
IN *MYZUS PERSICAE* SULZ. (APHIDIDAE; HOMOPTERA)

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Quaestiones entomologicae
4 : 3 - 29 1968

Adult apterous aphids, *Myzus persicae* Sulz., were raised on discs of radish and cabbage leaves to determine the effect of different population densities on the proportion of alate offspring produced. Parents in the higher density treatments produced a greater proportion of alate offspring. It is thought that this was a result of the crowding of the young instars as well as the crowding of the parents. Parents fed on cabbage produced a greater proportion of alate offspring than did those on radish. The fecundity of the adults and the survival of the offspring were reduced when fed on cabbage.

An effect of crowding was imitated by stroking the dorsal surfaces of the head, thorax, fore and hind abdomen, sides of the abdomen, antennae, and legs of adult apterae. These procedures caused no increase in the proportion of alatae among the offspring. A slight response of questionable significance was obtained to stroking over the general dorsal surface. A few first and second instar larvae were also stroked; none became alate.

Temporarily starving and crowding young adult apterae did not cause them to produce more than a normal number of alate offspring. First instar larvae were crowded. If their parents had not been crowded, most developed into apterae. If their parents had been crowded, most became alatae. In the clone studied larvae remained indeterminate as regards wing development at least until the first moult and possibly until the second.

An association between conditions of crowding and the development of winged forms in aphids has been reported (Wadley 1923 in *Rhopalosiphum prunifolia* Fitch, Bonnemaison 1951 in *Myzus persicae* Sulz. and *Brevicoryne brassicae* L.). Lees (1959) suppressed alate production by raising *Megoura viciae* Buckton individually. In 1961 Lees reported that individually raised apterae which were producing only apterous offspring, produced alate offspring if they were crowded together in a test tube for 24 hours. Johnson (1965) presented substantial evidence that contact between two adults of *Aphis craccivora* Koch caused them to produce winged offspring. He concluded that mechanical rather than visual or olfactory contact effected the response. The dorsal rather than the ventral surface of the parent aphid was affected by the stimulus. Aphids kept together for periods of time as short as 1 minute produced alate larvae. Most of the parents which responded did so completely, that is, their offspring were all alate. Johnson attempted to effect an artificial mechanical stimulus by stroking adult aptera for 2 minutes with a brush. Aphids so treated produced a percentage of alate offspring intermediate between that of singly reared parents and parents which had been in physical contact with other adults. MacGillivray and Anderson (1958) reported that the development of wings in *Macrosiphum solanifolii* Ashm. was not a response to crowding. *Myzus persicae* Sulz. raised concurrently under the same conditions did not develop winged forms.

My original objective was to produce alate offspring by mechanically stimulating (stroking) their apterous parents. The purpose was to

determine whether the essential, functional component of the "effet de groupe" (Bonnemaison 1951) was physical contact among the crowded adult aphids. Concurrent with efforts to induce the production of alatae mechanically, adult apterae were raised under different degrees of crowding to insure that the particular clone studied responded to crowding by producing alate offspring. The results of the first few experiments forced a broadening of the basis of the general objective, which then became an investigation of the effects of intraspecific interaction on the development of wings in the aphid *Myzus persicae* Sulz.

METHODS AND MATERIALS - GENERAL

A clone of *Myzus persicae* was begun in early December 1964 with a single apterous virginopara taken from a radish plant in a greenhouse. The descendants of this individual were raised in a plywood cabinet, in a constant temperature room at 60 F. From March 1965 a Sherer Gro Lab growth chamber was used (500 foot candles at the leaf surface).

The aphids were reared on discs of radish leaf cut with an 18 mm cork borer. The discs were placed, dorsal surface down, on a column of wet cotton wool in a short glass tube. The aphids were contained on the ventral surface of the disc by means of a small cylindrical glass tube. An elastic band secured the cage and also pressed the disc of radish into the cotton wool and ensured contact between the disc and the water in the cotton. The glass tubes were placed in distilled water, in an aluminum tray. Each cage was 12 mm in diameter inside and 9 mm high, enclosing an area on the leaf of 113 mm²; the glass tube which supported the cotton wool was 35 mm in diameter and 32 mm high. Circles, cut from a nylon fabric (27 strands per mm), were glued with LePage's Pliobond to the tops of the glass cages (fig. 1). Each cage was identified by a number in wax pencil on the glass tube. At the end of each experiment, both cages and tubes were washed and the tubes were refilled with fresh cotton wool. The discs were cut from radish (*Raphanus sativus* L.) plants, variety Forcing Scarlet Globe, grown under natural lighting conditions during the summer. In the fall and winter supplemental artificial light was added to bring the photoperiod to 14 hours. Only vigorous, growing leaves were used. The photoperiod in the growth chamber was set at a constant 16 hours light per 24 hours for all the experiments. The temperature was set at 72 F for 16 hours and 55 F for the remaining 8 hours. The 16 hours at 72 F began 1 hour after the lights were switched on. The growth chamber malfunctioned twice during the series of experiments. Both times conditions were restored to normal within a few hours.

The leaf discs remained in suitable condition for 4-7 days, depending on the density of aphids feeding on them. Both adults and larvae were handled with a moist camel hair brush. The brush was inserted between the front legs from in front and the aphid was moved. Care was taken to avoid touching the dorsal surface.

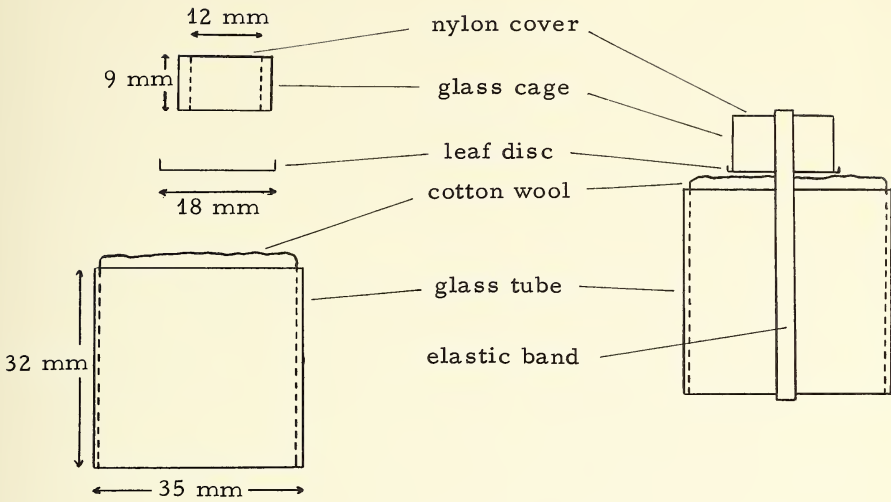


Fig. 1. Rearing cage.

EXPERIMENTS

Twenty five experiments were conducted; 4 on the effect of continuous crowding; 10 on the effect of stroking, 6 with adults and 4 with larvae; 11 on the effects of temporary crowding, 5 of adults from crowded parents, 3 of adults from parents raised singly and 3 of larvae from parents variously raised.

The data from all experiments were analyzed by means of an IBM 7040 computer, program number BMDO2V, an analysis of variance for factorial design. The death of individual aphids resulted in some missing values. Where there was one missing value in an experiment, an empirical value was substituted, calculated by the missing plots method of Goulden (1960). The experiments in which these calculations were made are noted below.

Crowding throughout Reproductive Period

Objective and methods

Adult aphids were subjected to different degrees of crowding during the entire reproductive period in an attempt to confirm that crowded parents produced more alate offspring than parents which were not crowded. Such treatment would also provide information on the relationships, if any, between the age of the parent and the degree of alate production, on the effects of crowding on the fecundity of the parents and on the survival rate of parents and offspring.

Aphids were reared under different population densities for the entire reproductive period. The aphids chosen as parents were selected in the fourth instar from leaf discs on which there were fewer than 10

individuals. When larviposition began, the parents were moved to new discs whenever the number of offspring exceeded 7. An attempt was made to limit the greatest number of offspring per disc to 15. As a result, parents in the greater densities were moved more often than those under less dense conditions. The parents in the lesser densities were picked up and put down when no moving was necessary in order to equalize, across all densities, the number of times parents were disturbed. The offspring were raised to maturity and the form of each, alate or apterous, was noted. A few intermediate forms were born. These were classed as alate.

Four experiments in which parents were crowded during the entire reproductive period were performed. The aphids for the third experiment were selected from among the last offspring of the second experiment and were kept within the density and replication of the parents. In the fourth experiment cabbage as well as radish was used as a host plant.

Results and Discussion

The results of the first experiment (table 1) confirmed the findings of Bonnemaison (1951). The increased proportion of alatae was a result of both an increase in the number of alatae born and a decrease in the number of aptera in the higher densities. The increase in alate offspring did not manifest itself statistically until after the first third of the reproductive period, although the tendency appeared earlier. The length of the reproductive period was much the same at all densities, averaging 21 days. The fecundity of the parents was unaffected by the increased population density, according to the statistical analysis ($F < 1$). However, the number 3 replicate of the solitary group was not a normal individual and perhaps should not have been included in the analysis. It produced 21 offspring, the average of the solitary aphids was 61.2. Aside from this value, there was no overlap between densities. The total offspring per parent per day did not show a statistical difference between densities, but a trend toward decreasing numbers of offspring with increasing parent population density was apparent.

In the first experiment, it seemed that a population density of 4 parents was sufficient to produce the desired effect, therefore, in the next experiment the 8 parent density was eliminated and a 2 parent density begun. The same trend in the proportion of the total offspring which were winged, was observed. In the intermediate density the proportion of alatae was closer to the control than to the highest density (table 2). Unlike the 1, 4, 8 experiment the increase of alatae was greatest in the first third of the reproductive period. The mean total number of offspring (56) was close to that of the 1, 4, 8 experiment (54). However, in the 1, 2, 4 experiment the single parents were the least fecund.

The additional data collected on the mean number of offspring per cage provided two interesting observations. First, although the number born per parent was highly variable (range 41-90), the percent survival was high (grand mean 87%). The second observation was the highly significant difference between treatments in the mean number of offspring per cage for the first third of the reproductive period and for the total period. In both these parameters the higher density parent

treatments had more offspring per cage (table 2). The third experiment used the second generation from the second experiment at the same densities (1, 2, 4). Two of the solitary parents died soon after the experiment was begun. Analyses of variance were done using a desk calculator. In response to the observation made in the first generation experiment on the mean number of offspring per cage, great care was taken to keep the size of the offspring groups fairly small; otherwise conditions were similar. The results of the second generation 1, 2, 4 experiment are given in table 3. The total number born per parent was even more variable than in experiment 2 (range 12-86); the average was 52. The per cent survival was high (88) and showed little variation (range 82-95%), as in the first generation. However, the per cent alatae differed from both earlier experiments and did not increase with increased parent population density. There was no statistical difference at $P = 0.5$ between the single parent treatment (10%) and the 4 parent treatment (12%). Very few more alate offspring were born to the crowded parents than to the parents raised singly. Two explanations of the contradiction in the results of the proportions of alatae are possible. The results of the second generation 1, 2, 4 experiment might be due to a "generation" effect. It is possible that the environment experienced by the grandparent (parents in experiment 2) affected the progeny of experiment 3. The phenomenon which makes such a situation possible is the telescoping of generations characteristic of aphids. Very often, the more mature embryos in a parent have within themselves developing embryos. Lees (1959) has shown that such a "generation" effect is possible in the production of sexuals. However, I do not think this is a satisfactory explanation here. If the stimulus which diverts an embryo toward becoming apterous also diverts embryos which it contains, then a first generation of aptera would have to be followed by a second generation of aptera. This is not so. Also, although the conditions under which the grandparents were kept as adults differed, the parents were raised to maturity under very similar conditions, i. e. between 5 and 10 individuals per radish disc.

A better explanation is the one suggested earlier from the results of the first 1, 2, 4 experiment. The size of the offspring group might have an effect on the number of larvae within that offspring group which developed wings. Very few of the offspring groups in experiment 3 exceeded 15. A χ^2 test (Goulden 1960) was performed testing the independence of size class of offspring groups (< 10, 10-15, > 15), and the number of alatae and apterae in these groups. In experiment 2 there was a marked association between a large offspring group and alatae, and a corresponding association between a small offspring group and apterae $\chi^2 = 123.9^{***}$. There were no such associations in experiment 3 ($\chi^2 = 2.46$).

If the association between a high proportion of alatae and a high larval population density is valid, then perhaps the initial premise that high parent population density is the principal cause of alate production is incorrect. That is, the postnatal environment rather than the prenatal environment with respect to crowding may be more or at least equally important. The lack of association between a high percentage of alates and a high larval population density in the second generation 1, 2, 4 ex-

periment could be interpreted as a threshold response. It may take more than 10-15 larvae to make a crowd.

TABLE 1. First crowding experiment. Mean numbers of alate and apterous offspring born to apterous parents raised singly or in groups of 4 or 8.

Segment of reproductive period	Number of offspring per parent			F	Grand mean
	1 parent	4 parents	8 parents		
1st third					
alate	4.0	10.2	9.2	4.07	7.8
apterous	16.5	8.0	3.0	5.63*	9.2
2nd third					
alate	3.0	17.5	14.2	30.55**	11.6
apterous	27.5	9.2	5.2	11.31**	14.0
Last third					
alate	1.2	4.2	7.8	15.24**	4.4
apterous	9.0	7.8	5.5	< 1	7.4
Total					
alate	8.2	32.0	31.2	64.46**	23.8
apterous	53.0	24.8	13.2	7.38*	30.3
Reproductive period in days	20.0	21.8	21.2	< 1	21.0
Total offspring:					
per day	3.1	2.6	2.1	< 1	2.6
maturing	61.2	56.8	44.5	< 1	54.2
% alate	16.4	56.6	70.0	101.16**	47.7

* = $P < .05$; ** = $P < .01$

Bonnemaison reported that *Myzus persicae* raised on radish produced more alatae than *M. persicae* raised on cabbage. If the hypothesis that alatae are a result of mechanical stimulation is correct, then there is an implication that aphids raised on radish are more restless than aphids raised on cabbage, i. e. that on cabbage there is less intraspecific interaction. Another implication is that singly raised aphids, whether on radish or cabbage, should give birth to few alate offspring. A fourth experiment was performed with these considerations in mind. The results (Awram 1966, table 5) were quite variable; however these observations could be made. On radish the pattern of results was similar to the first two experiments. The greater the population density of the parents, the greater was the proportion of winged offspring (22% for singly kept parents, 30% for parents kept in pairs, 43% for parents kept in groups of 4). Again the increased proportion of alatae was a result

of both an increase in alatae and a decrease in apterae in the high densities. On cabbage results were similar except that the mean proportion of alatae in the intermediate density exceeded that in the high density (34% alatae for singly kept parents, 58% for paired parents, 49% for parents kept in groups of 4).

TABLE 2. Second crowding experiment. Mean numbers of offspring born to apterous parents raised singly or in groups of 2 or 4.

Segment of re-productive period	Number of Offspring			F	Grand mean
	1 parent	2 parents	4 parents		
1st third					
alate	0.8	6.2	12.8	13.25**	6.6
apterous	15.8	16.2	11.2	3.00	14.1
mean per cage	11.2	13.8	24.0	34.78**	16.3
2nd third					
alate	2.5	9.2	10.0	1.90	7.2
apterous	12.2	11.2	9.8	< 1	11.1
mean per cage	16.5	16.2	21.0	3.66	17.9
Last third					
alate	3.0	3.5	3.8	< 1	3.4
apterous	14.5	15.5	11.5	1.59	13.8
mean per cage	12.8	12.5	13.2	< 1	12.8
Total					
alate	6.2	18.5	26.5	6.37*	17.1
apterous	42.5	42.8	32.5	2.83	39.2
mean per cage(av.)	13.2	14.2	19.0	31.72**	15.5
Total offspring reaching maturity	48.8	61.0	58.5	1.93	56.1
% survival	86.0	86.8	88.3	< 1	87.0
% alate	14.9	27.3	46.2	8.13*	29.4

* = $P < .05$; ** = $P < .01$

Bonnemaison's observations with respect to host plant were not confirmed; in fact, the opposite result was obtained. Both the 2 and 4 parent densities on cabbage (58%, 49%, respectively) had a greater proportion of alatae than the corresponding radish densities (30%, 43% respectively). The hypothesis that intraspecific interaction maintains alate

production is, however, not disproved. The effects of radish and cabbage are just reversed. That cabbage was a less desirable host plant could not be doubted. The per cent survival on radish was characteristically high at 91.2 as compared to 71.7 on cabbage. The fecundity of the parents was also affected. The number born was less on cabbage than on radish. Cabbage would presumably result in restless aphids, there would be greater intraspecific interaction and thus a greater percentage of winged individuals.

χ^2 test for independence on the data of the fourth experiment again indicated an association between a high proportion of alatae and a high larval population density ($\chi^2 = 71.36^{**}$).

TABLE 3. Third crowding experiment. Mean numbers of offspring born to apterous parents raised singly or in groups of 2 or 4.

Segment of re-productive period	Number of Offspring			F	Grand mean
	1 parent	2 parents	4 parents		
1st third					
alate	1.0	0.5	3.2		1.7
apterous	14.0	13.0	18.8		15.5
mean per cage	10.5	10.2	12.2		11.1
2nd third					
alate	0.5	0.5	2.5		1.3
apterous	11.0	13.2	19.2		15.2
mean per cage	10.0	11.8	15.2		12.8
Last third					
alate	1.5	0.2	0.5		0.6
apterous	11.5	10.5	11.0		10.9
mean per cage	8.5	12.0	11.8		11.2
Total					
alate	4.0	2.0	6.8	4.79	4.1
apterous	36.5	36.6	48.5	< 1	41.4
mean per cage	9.0	10.8	13.2	3.40	11.4
Total offspring reaching maturity	39.5	38.2	55.2	0.73	45.3
% survival	93.8	84.4	87.4		87.5
% alate	9.6	4.2	12.2	2.79	8.5

Stroking

Objective and methods

One of the more obvious effects of crowding is increased physical contact among the individuals crowded. The mechanical stimulation resulting from this increased contact might influence wing morphogenesis. If mechanical stimulation is the principal factor eliciting the production of alatae, then stroking the adults or the early instar larvae or both should produce more winged forms. Aphids were stroked at various frequencies, over the entire dorsum and over particular parts of the dorsum, to determine if alate production could be so induced (or more properly if apterae production could be reduced) and to find out if a particular area was especially sensitive.

Adults - Fourth instar larvae were removed from offspring groups of 10 or fewer individuals and confined alone in separate cages on radish discs. Stroking began after they had moulted into the adult but before they had offspring, or on the first day that offspring were born. They were stroked at different frequencies with either the leg of an apterous aphid, a *Drosophila* leg, or a human hair. The direction of stroking was more or less caudad, with the tarsal claws of the legs raked over the area being stroked. The aphid and *Drosophila* legs and the hair were manipulated with fine forceps under X 12 power of a stereo binocular microscope. Some treatments consisted of timed contact with a live adult aphid which had been mounted with paraffin on a pin. The parent aphids were moved when their offspring numbered more than 7, usually every second day. In the first experiment only, parents were moved almost daily.

There were 3 treatments and a control and 4 replicates in each experiment. Missing values calculations were made for 1 replicate each in the third, fourth, and fifth experiments. In the first experiment 100 strokes were applied daily with a hair, a *Drosophila* leg, and the leg of an adult aphid respectively to the entire dorsal surface. In the second experiment one batch spent 2 minutes daily in contact with a live adult aphid, the other two received 300 strokes daily with the leg of an adult aphid, and with a hair respectively, again on the entire dorsal surface. In the third experiment 500 strokes daily were applied with the leg of an adult aphid to the head, the thorax, and the abdomen respectively. In the fourth experiment 400 strokes were applied daily with the leg of an adult aphid to the hind half of the abdomen, the front half of the abdomen, and to the legs respectively. In the fifth experiment 500 strokes were applied daily with the leg of an adult aphid to the antennae and to the sides of the abdomen, and with a hair to the entire dorsal surface. In the final experiment one batch had 1000 strokes applied daily to the entire dorsal surface with the leg of an adult aphid, one had 5 minutes daily contact with a live adult aphid, and the last had a twice daily smearing with cornicle secretion.

Larvae - The association revealed in all crowding experiments except the third between a high proportion of alate offspring and a large offspring group, provided a basis for suspecting that in *M. persicae*, the postnatal environment may be of greater consequence than prenatal conditions. Four experiments were done to test this suspicion. First and

second instar larvae were stroked at different frequencies with a detached aphid leg. Larvae so treated were of 2 types, either from uncrowded (first 2 experiments) or from crowded (last 2 experiments) parents. They were removed from the parent within 8 hours of birth and raised to maturity alone. The first two experiments were the same; from 3 to 5 aphids were in each batch. One batch was stroked 500 times in the first instar, one batch 500 times in first and second instars, a third batch served as an un-stroked control. The last two experiments depended on the results of the first two and are described below under that heading.

Results and discussion

Adults - In the first adult stroking experiment (table 4), parents receiving 100 strokes daily with an aphid leg gave birth to a proportion of alate offspring much greater than others. The higher percentage of alatae was a result more of increased alate births than of decreased apterous births. In the first third of the reproductive period the number of alate offspring was about the same as in the other treatments; by the last third, the increased incidence of alate offspring was of statistical significance. The length of the reproductive period was about the same for all treatments, averaging 12.8 days. The total offspring reaching maturity during the experiment averaged 47.7 per parent but varied from 6 to 78.

TABLE 4. First adult stroking experiment. Mean numbers of offspring born to apterous parents stroked 100 times daily with a hair, a *Drosophila* leg, or an aphid leg.

Segment of reproductive period	100 strokes hair	100 strokes <i>Drosophila</i> leg	100 strokes aphid leg	Control	F
1st third					
alate	1.5	1.2	0.2	1.5	< 1
apterous	14.0	11.0	9.2	15.2	1.02
2nd third					
alate	1.5	2.0	7.0	4.8	2.99
apterous	16.0	12.5	7.4	13.2	< 1
Last third					
alate	3.5	1.8	9.5	1.5	5.90*
apterous	15.2	14.0	11.5	15.2	< 1
Total					
alate	6.5	5.0	16.8	7.8	7.93**
apterous	45.2	37.5	28.2	43.8	< 1
reaching maturity	51.8	42.5	45.0	51.5	< 1
% alate	9.8	9.6	41.4	14.3	14.53**

* = $P < .05$; ** = $P < .01$

For the second experiment (table 5) the *Drosophila* leg was dropped as a stroking device because of its poor utility as such an instrument and because it seemed no more effective than the hair. The difference between treatments, with respect to proportion of alatae, narrowly missed statistical significance at $P < 0.05$. The percentage of alatae was greatest from parents which had contact with a live aphid, next from those stroked with an aphid leg, then those stroked with a hair, and least from the un-stroked control. This supports the hypothesis that alatae are determined by intraspecific interaction. The argument is further supported by the numbers of alatae and apterae in each treatment during each third of the reproductive period. The mean size of the offspring groups was greatest from adults stroked with a hair, however these gave the second lowest proportion of alate offspring. The rate of survival was characteristically high with a grand mean of 89%.

TABLE 5. Second adult stroking experiment. Numbers of offspring born to apterous parents stroked daily with an aphid leg or a hair or kept in contact with a live aphid for 2 minutes.

	Treatment Description				F
	Control	2 minutes contact with live aphid	300 strokes aphid leg	300 strokes with hair	
Total number of offspring					
alate	8.0	19.0	12.2	14.2	1.33
apterous	30.0	20.2	20.0	40.0	3.93*
reaching maturity	38.0	39.2	32.2	54.2	1.59
Mean per cage	12.0	12.5	13.0	16.2	10.99**
% survival	82.3	96.0	85.4	90.8	3.85
% alate	17.4	46.1	38.0	26.3	3.70

* = $P < .05$; ** = $P < .01$

The frequency of stroking in this second experiment was 3 times that in the first, yet there was not a corresponding increase in the effect which the stroking was presumed to induce. However, I viewed the results optimistically and reasoned as follows. If mechanical stimulation was the cause of alatae production, then perhaps there was some special area of the body most receptive to such stimulation. The next 3 experiments were designed to explore this. Concentration of stroking in a small area would also have the effect of increasing the intensity of the treatment. I hoped that the dorsal abdominal area would be a sensitive one because the often observed phenomenon of alatae giving birth only to apterae might then be explained; receptors on the abdomen would be

covered by the wings and could not therefore be stimulated.

The results (tables 6, 7 and 8) were disappointing. In the first 2 experiments the controls had the highest proportion of alatae. In the last experiment the controls had the second highest, being slightly exceeded by those given 500 strokes to the antennae. In none of these 3 experiments was there any statistical difference of consequence in alate production. The per cent alatae increased through the 3 experiments. There was a corresponding increase in the average size of the offspring group and in the per cent survival. A χ^2 test was performed to determine if there was an association between the type of progeny and the size of the offspring groups. The χ^2 values were respectively 2.66, 10.01**, 51.08**.

TABLE 6. Third adult stroking experiment. Numbers of offspring born to apterous parents stroked on head, thorax, or abdomen.

	Treatment Description				F
	500 strokes head	500 strokes thorax	500 strokes abdomen	Control	
Total number of offspring					
alate	5.5	1.5	3.2	3.2	1.53
apterous	38.8	28.0	23.8	21.8	2.53
reaching maturity	44.2	29.5	22.0	25.0	2.68
Mean per cage	10.2	9.0	7.8	9.8	2.83
% survival	93.4	77.7	82.5	80.8	< 1
% alate	13.1	6.6	8.7	15.4	1.05

The results of the 3 experiments on regional stroking caused me to doubt my original success with the first 2 stroking experiments. A final experiment was done to confirm or refute this success. The cornicle secretion treatment was introduced to round off the experiment to 4 treatments. Since it is possible that the intraspecific interaction is of a chemical as well as, or rather than, a mechanical nature, I thought it worth trying this most obvious secretion. Cornicle exudate from roughly handled aphids was brushed against the aphids and solidified almost immediately; by the end of the experiment, these parents were coated with the hardened secretion.

The differences (table 9) in the per cent alatae were not statistically significant, but the treatments rank in much the same order as in the first experiments so far as these are comparable. Again the number of alatae and apterae corresponded to what would reasonably be expected. The live aphid and stroking treatments had more alate offspring

and less apterous offspring than the control. The control had the least alate and the most apterous offspring. Statistical significance was reached in the differences in apterous offspring in the second and third batches of offspring. The cornicle secretion treatment was ineffective.

TABLE 7. Fourth adult stroking experiment. Numbers of offspring born to apterous parents stroked daily.

	Treatment Description				F
	400 strokes hind abd.	400 strokes fore abd.	400 strokes legs	Control	
Total number of offspring					
alate	7.0	11.8	7.0	13.2	1.95
apterous	48.0	48.0	32.0	35.0	1.57
reaching maturity	55.0	59.8	39.0	48.2	1.14
Mean per cage	10.5	10.2	9.0	10.8	2.24
% survival	87.5	85.6	78.6	92.0	< 1
% alate	12.0	19.8	12.8	27.1	3.83

TABLE 8. Fifth adult stroking experiment. Numbers of offspring born to apterous parents stroked 500 times daily.

	Treatment Description				F
	Control	500 strokes antennae with aphid leg	500 strokes sides of abdomen with aphid leg	500 strokes dorsum with hair	
Total number of offspring					
alate	23.5	18.2	14.5	20.8	1.11
apterous	46.8	39.8	55.2	62.5	3.57
reaching maturity	70.2	58.0	69.8	83.2	4.60*
Mean per cage	17.2	15.5	15.0	15.2	1.88
% survival	94.3	96.6	91.3	94.9	1.60
% alate	32.9	33.5	21.8	24.0	1.35

* = $P < .05$

TABLE 9. Sixth adult stroking experiment. Numbers of offspring born to apterous parents variously treated daily.

	Treatment Description				F
	1000 strokes dorsum with aphid leg	5 minutes contact live aphid	Cornicle secretion twice daily	Control	
Total number of offspring alate	10.8	16.2	6.0	4.8	2.78
apterous	29.8	27.0	30.2	38.8	2.52
reaching maturity	40.5	43.2	36.2	43.5	< 1
Mean per cage	11.5	13.2	11.2	12.8	2.30
% survival	92.4	90.1	87.0	86.0	< 1
% alate	24.4	37.4	16.8	10.5	2.71

Reasons for the conflicting results obtained in the stroking experiments were not obvious to me. There appeared to be a response to general stroking over the entire dorsal surface. I can offer no explanation why a stroking frequency of only 100 strokes per day was much more effective than 300 or 1000 strokes per day. The lack of response when stroking was restricted to particular areas implies that the sensitive area, if such an area exists, was missed. This seems unlikely because the areas chosen covered most of the dorsal surface.

Larvae - I have followed a general tendency to think in terms of establishing conditions that result in the production of alatae. As Johnson and Birks (1960) have stressed, one should think in terms of conditions that result in the production of apterae. The embryo probably begins its development toward an alate form. Along its developmental path, it encounters conditions which may keep it on the path to becoming alate or "switch" it into an apterous pathway. Such a switch may be irreversible. This means that conditions designed to maintain an embryo or larva on the alate path may be imposed in vain if that embryo or larva has already been switched to the apterous path. The first two larval stroking experiments may have suffered from this oversight since they were done with the progeny of a single parent which had been raised under uncrowded conditions. None became alate.

Two further experiments were therefore done for which the parents were under very crowded conditions (17 per 50 mm²) for 4 days before the experiments began. The offspring of 3 of these parents were used for 3 aphid leg stroking treatments and a control in the first experiment and 4 treatments and a control in the second. In the first 200 strokes 3 times in the first instar, in the second instar, and in both of these instars were applied. In the second 300 strokes once in the first

instar, 300 strokes twice in the first instar, 300 strokes once in the first and in the second instar, and 300 strokes once in the first and twice in the second instar were applied. None developed into alatae. The offspring, all apterae, were kept and the first 2 batches of their offspring were collected and raised to maturity. No third generation effects could be observed with respect to the proportion of alatae born (Awram 1966, tables 17 and 18).

Temporary Crowding

Objective and methods

The results which Lees (1961, *M. viciae*) and Johnson (1965, *A. craccivora*) reported on the effect of temporary crowding were unequivocal. In *M. viciae*, individuals which had been producing essentially all apterous offspring switched completely to the production of essentially all alate offspring after they had been crowded for 24 hours. In *A. craccivora*, Johnson found that a similar change could occur after as little as 1 or 2 minutes contact between as few as 2 aphids. I tried similar temporary crowding experiments to clarify the confusing results which I obtained in the rearing and stroking experiments.

Adult aphids were crowded at different densities, for different periods of time away from the host plant in an attempt to induce the production of alate forms. It was hoped to learn the smallest amount of "togetherness" which evoked a response. First and second instar larvae were also crowded for short periods to determine whether or not high postnatal population densities could maintain the larvae on the path to the alate condition.

Adults - Adult aphids were crowded in the standard sized cage previously described, and also in a small cage 8 mm in diameter (inside measurement) and 9 mm high, enclosing an area on the leaf of 50 mm², and in microtubes 4 mm in diameter and 7 mm long (inside measurements). They were maintained in these containers on moist cotton. No leaf discs were available to them during the period of their confinement. After a set period of time, they were placed on fresh leaf discs and kept individually. Their first 2 batches of offspring were raised to maturity and the form they had taken was noted. All other conditions were similar to those described above under methods and materials - general. The periods of crowding which lasted less than 16 hours were imposed during the day. The 16 hour periods included 8 hours of night. Because of the lack of time and space, not all 16 of the aphids crowded 16 together could be used; 4 were selected to represent that treatment. A detailed description of the temporary crowding experiments follows.

There were 4 replicates in each treatment in each of the five experiments with adults from crowded parents. One estimate for a missing value was calculated in each of the 4 and 16 hour treatments in the second experiment. In the first temporary crowding experiment single aphids were kept in the microtube overnight (about 12 hours), and groups of 4 aphids were kept in the microtube 1 hour, and overnight (about 12 hours) (table 10). In the other four experiments all aphids were crowded and held in the standard sized cage (see materials & methods - general). In the second temporary crowding experiment 1 aphid was kept alone away from the host plant for 1 hour, for 2 hours, for 4 hours, and for 16 hours

(table 11). The third (table 12), fourth (table 13), and fifth (table 14) experiments on temporary crowding were the same except 2, 4, and 16 aphids respectively were crowded away from the host plant for the same time periods.

TABLE 10. First experiment on temporary crowding of adults from crowded parents. Numbers of offspring born to apterous parents kept alone or 4 together in microtubes.

	Treatment Description			F
	1 aphid in microtube overnight	4 aphids in microtube 1 hr.	4 aphids in microtube overnight	
Number of offspring alate				
1st batch	5.8	6.0	2.8	5.66*
total	11.8	23.8	15.8	3.21
apterous				
1st batch	5.5	10.2	10.0	4.92*
total	28.2	42.0	42.5	3.90*
reaching maturity mean per cage	40.0	65.8	58.2	8.07*
1st batch	14.5	17.8	13.8	1.70
total	11.0	13.8	13.2	2.25
% survival	74.0	94.3	89.6	7.17
% alate	29.5	36.2	27.1	1.19

* = $P < .05$

TABLE 11. Second experiment on temporary crowding of adults from crowded parents - control, uncrowded. Numbers of offspring born to apterous parents starved alone for 1, 2, 4, or 16 hours.

	Treatment Description			
	alone 1 hr.	alone 2 hr.	alone 4 hr.	alone 16 hr.
Number of offspring alate	2.8	10.0	6.0	9.0
apterous	16.2	19.8	16.7	21.3
reaching maturity mean per cage	19.0	29.8	22.7	30.3
	13.0	16.2	14.7	19.0
% survival	71.3	91.0	80.0	81.5
% alate	16.9	32.4	26.4	28.5

TABLE 12. Third experiment on temporary crowding of adults from crowded parents. Numbers of offspring born to apterous adults crowded 2 together for 1, 2, 4, or 16 hours.

	Treatment Description				F
	2 crowded 1 hour	2 crowded 2 hours	2 crowded 4 hours	2 crowded 16 hours	
Number of offspring alate					
1st batch	2.0	1.0	4.8	8.2	6.66*
2nd batch	1.5	2.5	0.2	2.0	2.03
total	3.5	3.5	5.0	10.2	3.44
Number of offspring apterous					
1st batch	9.2	10.8	11.2	5.2	1.28
2nd batch	6.5	7.0	3.8	19.8	14.36**
total	15.8	17.8	15.0	25.0	1.29
mean per cage					
1st batch	14.0	12.5	20.5	14.8	1.40
2nd batch	8.2	10.0	7.5	25.0	13.14**
total	11.0	12.0	17.5	20.0	2.23
% survival	86.4	90.9	76.2	88.5	1.86
% alate	22.1	16.1	20.8	30.6	1.05

* = $P < .05$; ** = $P < .01$

Three experiments were done on the effect of temporary crowding of adults from parents raised singly. Only a control and the most intense crowding were used. First instar larvae from uncrowded parents were raised to maturity individually. In the first experiment 8 were then maintained separately as controls, 16 were crowded together for 16 hours (16 per 113 mm²), after which they were again kept separately. The first several batches of offspring were collected and raised to maturity. The second experiment was the same except that only 4 controls were used and of the 16 crowded together, 8 were selected as progenitors. The 16 aphids were crowded in the small cage (50 mm²). The use of the small cage increased the effective population density by a factor of 2.25 (table 15). The third experiment was identical except that the aphids were crowded in their fourth instar, rather than as newly emerged adults (table 16).

Larvae - In 3 experiments first instar larvae less than 12 to 24 hours old were crowded in the small cage for 12, 16 or 24 hours at densities of 16, 32 or 48 per 50 mm² (table 17).

TABLE 13. Fourth experiment on temporary crowding of adults from crowded parents. Numbers of offspring born to apterous parents crowded 4 together for 1, 2, 4, or 16 hours.

	Treatment Description				F
	4 crowded 1 hour	4 crowded 2 hours	4 crowded 4 hours	4 crowded 16 hours	
Number of offspring alate					
1st batch	2.8	3.8	0.6	9.0	7.07**
2nd batch	0.8	3.2	0.0	3.5	3.17
total	3.5	7.0	0.5	12.5	6.70*
Number of offspring apterous					
1st batch	16.5	16.0	11.2	7.2	3.79
2nd batch	12.8	6.8	9.2	22.5	13.92**
total	29.2	22.8	20.5	29.8	1.73
mean per cage					
1st batch	21.2	22.8	17.0	18.0	< 1
2nd batch	14.0	9.8	11.0	27.5	13.34**
total	17.5	16.2	14.2	22.8	1.94
reaching maturity	32.8	29.8	21.0	42.2	3.37
% survival	93.0	93.8	75.3	92.3	2.26
% alate	11.3	20.6	2.7	28.8	11.09**

TABLE 14. Fifth experiment on temporary crowding of adults from crowded parents. Numbers of offspring born to apterous parents crowded 16 together for 1, 2, 4, or 16 hours.

Number of offspring	16 crowded	16 crowded	16 crowded	16 crowded	F
	1 hour	2 hours	4 hours	16 hours	
alate					
1st batch	3.5	4.0	1.2	4.8	1.40
2nd batch	2.5	4.0	0.5	8.2	1.41
total	6.0	8.0	1.8	13.0	2.10
apterous					
1st batch	10.8	14.8	6.5	9.8	3.25
2nd batch	10.5	9.8	3.2	11.2	1.99
total	21.2	24.5	9.8	21.0	2.62
per cage (av.)					
1st batch	17.0	20.8	12.8	16.2	3.51
2nd batch	14.8	15.0	3.8	22.0	8.52*
total	16.0	17.8	9.2	18.8	6.10*
reaching maturity	27.2	32.5	11.5	34.0	10.52**
% survival	86.0	92.1	59.0	89.6	4.51
% alate	26.0	22.4	16.8	37.6	< 1

* = $P < .05$; ** = $P < .01$

TABLE 15. First and second experiments on temporary crowding of adults from parents raised singly. Numbers of offspring born to apterous parents kept individually or crowded 16 together.

Number of offspring	8 adults kept individually	16 adults 16 hours small cage	16 adults 16 hours large cage	t
alate				
1st exp.	26.3		18.7	0.01
2nd exp.	13.8	6.6		0.36
apterous				
1st exp.	42.6		43.2	0.63
2nd exp.	16.0	20.4		0.27
reaching maturity				
1st exp.	68.9		61.9	0.44
2nd exp.	29.8	27.0		1.29
per cage (av.)				
1st exp.	18.3		17.3	0.29
2nd exp.	16.8	14.9		0.26
% survival				
1st exp.	94.2		93.8	0.15
2nd exp.	89.8		91.4	2.40
% alate				
1st exp.	38.0		30.0	1.02
2nd exp.	45.4	24.2		2.54

TABLE 16. Third experiment on temporary crowding of adults from parents raised singly. Numbers of offspring born to apterous parents crowded 16 together for 4 hours in their fourth instars.

Number of offspring	Control	16 crowded 4 hours	t
alate			
1st batch	1.8	3.2	0.32
2nd batch	0	6.2	2.28
total	1.8	9.5	1.62
apterous			
1st batch	15.2	13.5	0.65
2nd batch	17.8	13.8	1.54
total	33.0	27.2	0.36
per cage (av.)			
1st batch	18.5	18.1	0.73
2nd batch	20.0	22.8	2.68*
total	19.5	20.4	0.56
% survival	90.4	90.4	0.85
% alate	4.9	25.0	2.96*

* = $P < .05$

TABLE 17. χ^2 for independence between crowded and uncrowded larvae, and development into the apterous or alate state. Results of temporary crowding of larvae from uncrowded parents (above) and from crowded parents (below).

	Apterous		Alate		
	Observed	Expected	Observed	Expected	
Parents uncrowded					
Control - raised singly	3	2.25	2	2.75	= 0.61
Treated - 16/50 mm ²	6	6.75	9	8.25	
Control	6	4.29	0	1.71	= 3.34
Treated - 32/50 mm ²	9	10.71	6	4.29	
Parents crowded					
Control	6	3.3	0	2.70	= 6.19*
Treated - 48/50 mm ²	10	12.7	13	10.30	

* = $P < .05$

Results and discussion

Adults - In the first temporary crowding experiment (table 10) no difference in the proportion of alate offspring among the treatments could be observed. The per cent alatae was almost identical in the aphids kept individually and in those crowded together in a microtube. Four crowded for 1 hour had the greatest proportion of alatae but the difference was not significant. The significantly high F values obtained for the first batch apterous, total offspring, and total apterous were, I think, a result of the unusually small per cent survival of those kept singly (74%).

From the second experiment (table 11) with single aphids off the host for different times, many results were missing so that this could not be analyzed by the IBM program. Only the means are given. This was essentially a test of the effect of different periods of temporary starvation on the production of offspring. No pattern could be observed in any of the measurements taken. The number of alate offspring, the number of apterous offspring, the total number of offspring, the proportion of offspring which were alate, the total offspring born and the per cent survival were not noticeably affected by 1, 2, 4, or 16 hours of starvation.

The results of the third experiment (table 12) were similar to those of the second temporary crowding experiment. There appeared to be no association between the proportion of alatae produced and the length of time that 2 parent aphids were in the same cage with one another. The exception to this general observation was the number of alate offspring in the first batch. Significantly more alate (8.2) were born to individuals caged together for 16 hours than to those caged for 1 and 2 hours. An intermediate number (4.8) was born to the individuals in the intermediate treatment (4 hours). The significant F values for the second batch of

apterae was probably a result of the zero values for replicates 1 and 2 in this treatment. These would probably be best viewed as missing values. The significant F value for the size of the offspring group of the second batch also reflected the zero of replicate 2 in this treatment. The large number of offspring per cage from those crowded for 16 hours might be suspected as the cause of the high per cent alatae of this treatment. However, the second batch here was almost all apterous.

A number of the parameters in the experiment with groups of 4 off the host (table 13) displayed statistically significant differences among the treatments. Most important of these was the total per cent alatae. The proportion of winged offspring was greatest after 16 hours crowding. The percentage after 1 hour crowding was considerably less and that after 2 hours crowding was intermediate. However the pattern was broken by the 4 hours crowding which gave the lowest per cent alatae. The situation was the same for alate offspring in the first batch, the 4 hour treatment falling outside the pattern. The difference between treatments shown by the number of apterous offspring in the second batch was a manifestation of the unusually high fecundity of the individuals crowded for 16 hours, which gave a much higher average number of offspring per cage in the second batch than the other treatments. The large size of the offspring group was not associated with a corresponding increase in alatae.

The experiment with groups of 16 (table 14) completed the symmetry of the experimental design of the crowding experiments. There was no difference between treatments in the number of alatae or apterae produced or in the per cent alatae. The significance attained with respect to total offspring, average, and second day size of offspring group and the total born was caused by the partial sterility and low survival rate of the individuals crowded for 4 hours.

The data obtained from the latter four experiments on temporary crowding of adults from crowded parents differed from some of the results obtained by Lees and Johnson. Several explanations are possible. Both these workers had raised the parent aphids used in their experiments separately. Mine were taken from groups of 10 or fewer individuals. The results I obtained may have been confounded by this previous association. Another possible explanation is that the density of parents was not great enough. It is possible that the 16 aphids would not encounter one another often enough to produce a response. A third explanation might be that the 4 individuals selected to represent the 16 of the high density treatments had never been walked upon, i. e. had themselves been the most active. Still another possible explanation is that I did not use enough replicates. The last three experiments were performed to correct these possible defects. Because there were only 2 treatments in each of these experiments, t rather than F values were calculated.

In the first experiment one of the control parents and 2 of the treated parents did not survive long enough to produce offspring. There was little difference (table 15) between the 2 treatments in any of the measurements taken in either of the first two experiments. Both control groups had the higher proportion of alatae, 38% against 30% in the first and 45% to 24% in the second experiment. As in the first experi-

ment with adults from parents raised singly, none of the measurements taken showed a significant difference between the controls and the treated individuals (table 15). Again, the controls had a greater per cent alatae than the treated aphids.

The results of the last experiment, in which aphids were crowded in their fourth instar, rather than as newly emerged adults are given in table 16. There is a significant difference in the proportion of alatae between the controls and the treatment parents, the treated having a greater per cent alatae. The greater proportion of alatae was a consequence of both more alatae in the treated and more apterae in the untreated group. The other significant factor was the size of the offspring group in the second batch. It was larger for the treated group and therefore postnatal effects could not be ruled out as a cause for the increased alate production.

Larvae - Crowding first instar larvae of comparatively uncrowded parents (raised in groups numbering less than 10) at a density of 16 per 50 mm² did not result in proportionately more becoming alate than among the uncrowded control individuals ($\chi^2 = 0.64$). Where the parents were raised individually for most of their lives, the difference in the proportion of alatae between crowded and uncrowded larvae appeared to be more definite, perhaps because the crowding was twice as severe as in the first experiment ($\chi^2 = 3.34$). The more intensive crowding still of the treated individuals in the last experiment resulted in a still larger proportion becoming alate ($\chi^2 = 6.19^*$). The effects of heavy parental crowding were apparently reversed in the control individuals.

GENERAL DISCUSSION

A few observations that transcended the 3 general types of experiments were made and are discussed here.

Fig. 2 is a plot of the per cent alate of control treatments against time. The variation was considerable and there was no discernible long term trend. Bonnemaïson (1951) found that over a 6 month period during which he experimented with *M. persicae*, there was a general tendency for increased alate production with increased age of the clone. This was not so in my experiments over the period June through December 1965.

No matter how careful I was to keep a parent isolated from other adults during both its infancy and adulthood, I was never able to prevent completely the occurrence of some alatae among its offspring. Fig. 2 illustrates the point. Never were the offspring of control parents entirely apterous. This implies that the production of a small proportion of alatae may be obligatory in the clone studied.

The rate of survival of offspring was high (average 88.1 per cent) in all of the experiments. An exception was the larvae which were stroked during their first and second instars, many of which died before reaching maturity. The survival rate of the parents was also high. Only 14 of 421 died before leaving 7 or more offspring.

The results I have obtained differ from Bonnemaïson's, Johnson's, and Lees' on several points. Rearing aphids under crowded conditions

temporary crowding of apterous parents resulted in an increased proportion of alate offspring. Mechanical stimulation of apterous parents by stroking did not result in a predictable increase in alate offspring. When a parent aphid seemingly responded to a treatment by producing alate offspring, it did not necessarily continue to produce alate offspring. A few examples, fig. 3, have been selected to illustrate this characteristic.

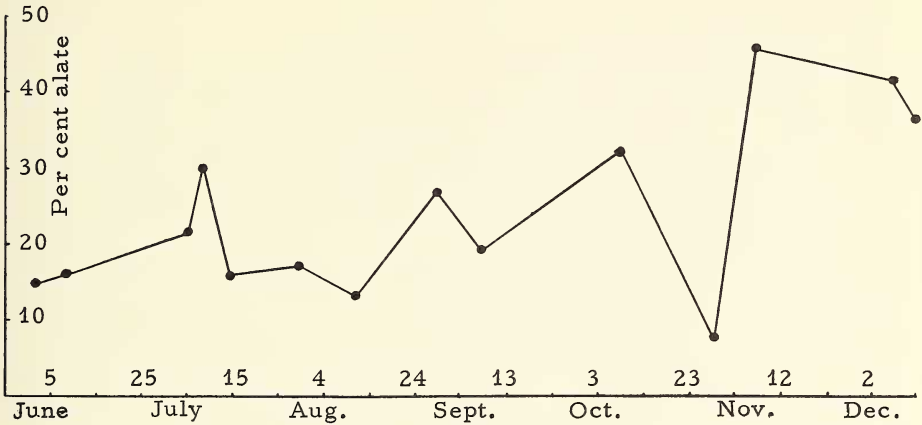


Fig. 2. Per cent alate in control treatments for June to December 1965.

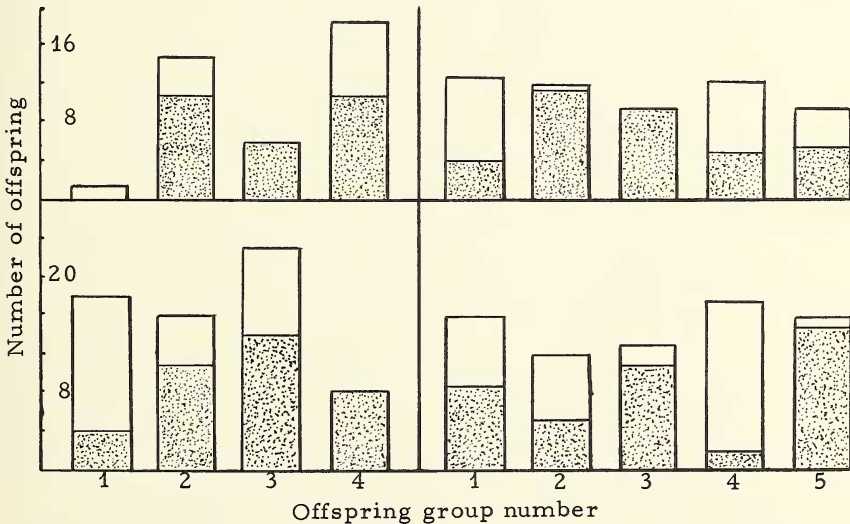


Fig. 3. Numbers and the ratio of alate to apterous offspring in consecutive batches born to individual parents of *M. persicae*; □ alate, ▒ apterous.

All of these contradictory results can be resolved if it is assumed that in the clone studied, the postnatal effects of population density were at least as important as the prenatal effects. The data obtained gave much support to this hypothesis. In almost all cases where a significant difference in per cent alatae between treatments was obtained, there was a corresponding association between a large offspring group size and a high proportion of alatae. Under the conditions of the experiments, about 15 larvae constituted a large enough population to produce a response.

If the hypothesis that postnatal crowding is at least as important as prenatal crowding is correct, then the ontogeny of an individual would follow one of the following pathways (Johnson and Birks 1960): if the parent is under crowded conditions, the embryo remains on the path toward becoming alate. After its birth, the larva may encounter crowded or uncrowded conditions; if crowded, it continues development toward becoming alate; if uncrowded, it is sidetracked and becomes apterous. If the parent is not crowded, then the embryo is sidetracked and irreversibly set on a developmental path leading to the apterous state, and is insensitive to conditions it encounters in its early instars. Alate offspring are obtained when parents and offspring (first and second instars) are subjected to crowding or conditions simulating crowding. The results of all experiments can be fitted into one or other of these hypothetical pathways. Table 18 illustrates the interaction of parent and offspring crowding and the type of offspring which would be formed if the pathways hypothesized exist. All the treatments are listed according to the parent offspring regime each encountered. An asterisk indicates a statistical significance between the treatment marked and the corresponding control treatment in respect of per cent alatae. All but one of the controls fall into the parent uncrowded-offspring uncrowded quadrant. All but one of the treatments which showed a significantly high proportion of alatae fall into the parent crowded-offspring crowded quadrant. Reasons for regarding this one exception (100 strokes daily with aphid leg) as anomalous have already been given. The data fit the hypothetical pathways.

The data and the hypothesis can be examined in the light of the characteristics of the life history of *M. persicae*. *M. persicae* is a dieocious aphid, that is, it has primary and secondary host plants between which it must travel to successfully complete its life history. Wings, twice a year, are necessary. It has the widest range of secondary plant hosts of any aphid. Therefore, winged forms of *M. persicae* are more likely than those of any other aphid to alight on suitable host plants. The percentage of seemingly obligate alatae which I observed, might thus be explained. *Aphis craccivora* and *Megoura viciae* the species used by Johnson and by Lees, are monocious and much more host specific than *M. persicae*.

There are adaptive advantages to maintaining the option of becoming alate or apterous until the first or second instars. A first or second instar larva that is still on the path toward the alate state, might, after a heavy rainstorm, find itself in uncrowded conditions. It would be to its reproductive advantage to be switched to the apterous state. Or an adult aptera might walk away from a crowded condition and deposit her

presumptive alate offspring in uncrowded circumstances. These could take advantage of such circumstances by being shunted to the path leading to the apterous state. This last instance is supported by one of the characteristics of *M. persicae*. Bonnemaïson (1954) found it to be a relatively "antisocial" aphid. *M. persicae* individuals tended to space themselves over the available surface of leaf, whereas *Brevicoryne brassicae* L., a more sociable type, remained in family groups.

CONCLUSION

The higher the population density of the *parents*, the greater was the proportion of alate offspring born to apterous *Myzus persicae* Sulz. But this general tendency can be overcome by preventing the size of the *offspring* groups from becoming too great. Apteræ raised on cabbage produced a greater proportion of alate offspring than apteræ raised on radish. The per cent survival of offspring reared on radish was high, near 90; on cabbage was lower, near 70. The fecundity of parents fed on cabbage was less than that of parents fed on radish. The fecundity and longevity of singly reared parents did not differ from that of parents reared in groups. No association between the physiological age of the parents and the tendency to produce alatae was observed.

An attempt was made to imitate physical contact among aphids by stroking individuals. Stroking adult, apterous aphids on the dorsal surface with a *Drosophila* leg or a human hair, at intensities of 100 or 300 strokes per day was ineffective in causing the aphids to produce alate offspring. Stroking particular parts of the body, with an aphid leg, at intensities of 400 or 500 strokes per day was also ineffective. Areas stroked included the head, thorax, fore and hind parts of the abdomen, the sides of the abdomen, the antennae, and the legs. Stroking applied generally to the entire dorsal surface at 300 or 1000 strokes per day may have caused a slight increase in alate production. One hundred strokes daily applied generally over the dorsal surface elicited a highly significant increase in the number of alate offspring. Two or 5 minutes daily contact of adult apteræ with other adults mounted live on a pin, caused a slight increase in the proportion of alate offspring born to them. There was an association, across the treatments of the stroking experiments, between a large number of offspring per cage and a large proportion of alate offspring.

Stroking first and second instar larvae at intensities of 200, 300 or 500 strokes once or twice per instar did not cause these larvae to develop into alatae. Offspring of these larvae were not disproportionately alate.

Starving young, adult apteræ for short periods (1, 2, 4 or 16 hours), did not affect the number of alate offspring produced. Crowding young, adult apteræ at population densities of 1, 2, 4 or 16 per 50 mm² for 1, 2, 4 or 16 hours did not result in an increased number of alate offspring. Crowding first instar larvae whose parents had been crowded, resulted in an increased number of them becoming alate.

In the clone studied, it was necessary for the first instar larvae

as well as their parents to be crowded before there was an increase in the number of alate individuals produced. The capacity to be channelled into the developmental pathway leading to the apterous state was retained beyond the embryo stage and well into the first and possibly second instars.

TABLE 18. A summary of the results, sorted into parents crowded or uncrowded and offspring crowded or uncrowded categories.

		P a r e n t s	
		Crowded	Uncrowded
C r o w d e d		Continuous, 4*, 8*; (1 / 8)** 2*, 4* radish, 2*, 4* cabbage; (2 / 9) Temporary, 2 for 1, 2, 4, 16 hr; (12/19) 4th instar 16 for 4 hr*; (16/21) 1st instar 48 for 24 hr*; (17/22)	Simulated***, 1st & 2nd instar 3 x 200; (- / 16) 1st & 2nd instar 300, 1st & 2nd instar 2 x 300; (- / 17) 1st & 2nd instar 500; (- / 12) Temporary, 2 for 1, 2, 4, & 16 hr; (12/19) 16/50 mm ² , 16 hr; (14/20)
	O f f s p r i n g		Continuous, 4; (3 / 10) Simulated, 100 with hair, <i>Drosophila</i> leg, & aphid leg*; (4 / 12) 300 with aphid leg, & hair; (5 / 13) 500, aphid leg on head, thorax, abdomen; (6 / 14) 400, aphid leg on hind abdomen, fore abdomen, & legs; (7 / 15) 500, aphid leg on antennae, sides of abdomen, & entire dorsum; (8 / 15) 1000, aphid leg on entire dorsum, cor- nicle secretion; (9 / 16) Temporary, 2 min with live aphid; (5 / 13) 5 min with live aphid; (9 / 16) 5 together 1 hr, 4 overnight; (10/18)
U n c r o w d e d			

* alate production significantly different from the control
 ** (table no. / page no.). (P < 0.05).
 *** crowding simulated by stroking.

ACKNOWLEDGMENT

I am grateful to Drs. W. G. Evans and B. Hocking for help given me in the execution of this work.

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